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Invited Paper

Colias alexandra: A Model for the Study of Natural Populations of Butterflies

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Abstract. Life tables constructed for a natural population of the Pierid butterfly *Colias alexandra*, analyzed key-factor techniques (for 1975-1979), show factors contributing to reduced natality determine the year to year population trends; these are largely density independent factors. These conclusions are consistent with the findings of similar studies and have been corroborated by two subsequent incidental events. The loss of an unusually large number of adult females in 1978 resulted in a population depression in the following year, which was continued for the next two years (e.g. from >.8 to <.4 eggs/sq m). In 1981, an outbreak of the predaceous free-running mite *Balaustium* sp. resulted in a 200% increase in egg mortality (approximately 30% to 60% of all eggs) without a subsequent overall decline in the population's adult (i.e. egg-laying individuals) numbers. The methods and findings of this and the limited number of comparable studies, which examine all life stages and span several years, produce a wealth of information about the individual system and provide a means of verifying the general theories of population ecology.

Introduction

Comprehensive observations of natural populations are necessary prerequisites for the verification of general theories of population ecology and for their subsequent application in management and conservation. Ideally observations should extend over a prolonged period and examine as many environmental factors (biotic and abiotic) as possible. Insects have proven to be useful subjects for the study of natural populations. It is surprising to find, however, as Gilbert and Singer state in their 1975 review of butterfly ecology, that relatively few contributions to insect ecology have come from butterfly research; that picture has only just begun to change (see Dempster, 1983; Strong, 1984). Butterflies, among the most visible of insects, have been important tools for testing and development of evolutionary theory (e.g. mimicry and polymorphism), yet there is a paucity of data regarding factors that limit or regulate butterfly populations. The more extensive studies of butterfly populations

have focused on adults (e.g. Ehrlich, 1965; Ehrlich and Gilbert, 1973; Brussard and Ehrlich, 1970; Brussard et al., 1974; Gilbert and Singer, 1973; Watt et al., 1977, 1979). These studies seriously neglect or ignore the wide range of selection forces that shape the remainder of the complex life cycle of these holometabolous insects. Adult population studies have not provided us with a general understanding of population regulation.

Critical to the complete understanding of the dynamics of a population is the assessment of its demographic attributes, such as the probability of survivorship at a given time or age class. These attributes reflect the adaptations of the population, such as the ability to procure resources, survive climatic extremes, and avoid predators. Notably few life tables, detailing reproduction and survivorship, have been constructed for butterflies (e.g., *Pieris rapae*, Richard, 1940; Harcourt, 1966; and Dempster, 1967; *Lycaena dispar*, Duffey, 1968; *Anthocharis cardamines*, Courtney and Duggan, 1983), although such demographic models have been applied to numerous other insect species. Insight into the causes of population fluctuations can be obtained when life tables can be coupled with an understanding of predation, parasitism, climate and other conditions that affect population numbers.

In the course of several papers, I have presented the findings to date of a continuing long-term study of a natural population of the sulfur butterfly *Colias alexandra* Edwards (Pieridae). I have been concerned with the identification of the demographic attributes of this population and the environmental factors which influence it (Hayes, 1981a & b, 1984), examining specific components of its life history (Hayes, 1982). The results of the study, which was initiated in 1975, represent a nearly unique set of data with regard to the investigation of butterfly population dynamics (see Singer and Gilbert, 1975; Dempster, 1983).

I have addressed two questions basic to understanding the dynamics of a population: 1) what causes fluctuations in the numbers of a species from year to year; and 2) what determines the magnitude of these fluctuations. On the basis of data obtained to date from this study, it is possible to begin to answer these questions, that is, to identify the factors which determine the abundance of this species and to examine the ecophysiological adaptations, such as dormancy, which may play a significant role in its distribution. The focus of this article is the determinants of abundance of *C. alexandra* and the implications for our current understanding of population regulation.

The System

Colias alexandra, first described by Edwards in 1873, is native to the Rocky Mountains and intermontane regions of North America. The taxonomy and distribution of the *C. alexandra* complex are discussed in detail by Brown (1973) and Ferris (1973). Discussions of other aspects of

the biology of this species can be found elsewhere, for example host plant preference (Ellis, 1973; Stanton, 1979), larval food plant use (Ae, 1958), adult nectar sources (Watt et al., 1974), and adult population structure (Watt et al., 1977).

The population examined in this study is univoltine (having one generation per year) and monophagous, utilizing only one larval food plant, *Lathyrus leucanthus* Rybd. (Leguminosae). In other populations *C. alexandra* utilizes other legumes and isolated bivoltine populations are known (Ellis, 1973; Hayes, 1981a, 1982). In the study population, females begin ovipositing in early July and continue through early August. Eggs are laid singly on the dorsal surface of the leaves of the food plant. Although specific egg distribution patterns have been associated with other so-called red-egg laying pierids (see Shapiro, 1981), there does not appear to be a consistent generation to generation pattern for this population of *C. alexandra* (Hayes, in prep.). No other Coliadine populations have been examined. There are two larval molts prior to the onset of winter conditions (i.e. regular nighttime freezing) in early September. In the third instar the larvae overwinter by entering diapause. Initiation of diapause is determined during the second instar as a response to cold temperatures ($\bar{x} \leq 24°C$; Hayes, 1982). Larval activity and development resume in late May, although the exact timing varies depending on weather conditions. There are two post-diapause or second season molts prior to pupation. Eclosion occurs in late June to early July, with males typically appearing earlier than females (Watt et al., 1977). The adults, and to a lesser extent the immature stages, may occur concomitantly with three other *Colias* species in this area: *C. scudderi, eriphyle* and *eurytheme*.

The Study Site and Field Methods

A relatively large population of *C. alexandra* occurs in the neighborhood of the Rocky Mountain Biological Laboratory (3200 m), near Crested Butte, Gunnison Co., Colorado. The population occupies fescue grassland/sagebrush habitats of the East River Valley (characterized by Langenheim, 1962). In order to accumulate information on the numbers and survivorship of *C. alexandra* during development from egg to larva to adult, a study plot was established in an area 13 kilometers southeast of Crested Butte along Brush Creek, elevation 2810 m, where adults and larval foodplant occur in relative abundance. This 20 x 20 m study plot is protected from grazing cattle by a three-strand barbed wire fence. The area actually surveyed encompasses 200 square meters, the vegetation within the plot being searched systematically in ten, 1 x 20 m strips. Plants with eggs or larvae are marked with numbered flags inserted into the ground next to them. A single plant usually provides adequate nutrition for a larva from hatching to diapause. Thus, individuals can be

followed to diapause by marking the location of the host plant. The survivorship, developmental rates, and activities of each egg or larva are monitored and recorded regularly at 48 to 72 hour intervals throughout the season. Post-diapause larvae are removed from the field plot and reared to eclosion in the laboratory. In this manner the incidence of parasitism, failure to pupate or eclose and the sex ratio can be determined. To avoid perturbing the study population, survivors were released at the study site. Post-diapause individuals outside the plot are observed to determine the incidence of predation and impact of inclement weather conditions. These basic techniques can easily be modified to conduct similar studies of other species.

Artificial populations can be created by releasing gravid females into flight cages (2x2x3 m) erected over natural vegetation. Adult *Colias* behave relatively normally within flight cages (Grula and Taylor, 1980; Silberglied and Taylor, 1972) and *C. alexandra* females oviposit freely (Hayes, 1981b). These artificial populations can be manipulated in a variety of ways without disturbing the natural population. For example, the effect of increased larval densities can be assessed by confining several ovipositing females at one time (Hayes, 1981b), or the effects of the presence of larvae of different ages on one another can be assessed by releasing gravid females into the cages at several-day intervals.

Wild-caught females will also oviposit under laboratory conditions. Although few matings have been obtained in the laboratory, *C. alexandra* have been reared successfully from egg to adult on a variety of host plants, clippings and an artificial diet (Taylor et al., 1981). Rearing within a controlled laboratory environment has facilitated the detailed study of several aspects of the behavioral ecology of *Colias* such as host preference (Stanton, 1979), food plant usage (Ae, 1958), and diapause dynamics (Hayes, 1982).

Results to Date

Age-specific or horizontal life tables were constructed for each year from 1975 to 1979 and 1981 (Table 1). The number of individuals entering each lifestage are recorded for each year. Age-specific life tables provide far more information than time-specific tables, but can only be used when a cohort is followed at close intervals throughout its life (see Southwood, 1976). In order to understand the effects that any one environmental factor has on population trends, a series of age-specific tables covering a number of generations is required. A number of different techniques have been used to analyze life table data in order to assess the effect of each component of the environment. The life table data for *C. alexandra* were analyzed by key-factor analysis techniques (Fig. 1; Varley and Gradwell, 1960). Key factor (also called K or killing factor) analysis is a concept originally introduced by Haldane (1949) and applied by Morris (1959)

Table 1. Age-specific life tables for *Colias alexandra* (1975-1979, 1981). The population occurs 13 km southeast of Crested Butte, Colorado, elevation 2810 m.

	Number Entering Each Stage					
Stage	**1975**	**1976**	**1977**	**1978**	**1979**	**1981**
eggs laid	68	181	371	386	157	99
larvae hatching	42	108	277	259	97	17
second instar larvae	20	68	134	177	61	12
third instar larvae	8	36	87	128	32	8
diapause	4	22	32	37	21	—
post-diapause	2	1	6	5	—	—
adults	2	1	3	2	—	—

and Varley and Gradwell (1960) to statistical methods for identifying the age-specific causes of population change. The k-value for mortality during each life stage is the difference between the common logarithms of the number of individuals entering that stage and the subsequent one. The total generation mortality is calculated by adding all the k-values. The k-values for each life stage over a number of generation are plotted against time. The total generation mortality caused entirely or in part by a key factor at a specific age can be seen by inspection of the inflections of the curve (or statistically with limitation, see Smith, 1973) since its k-value will change with time in the same manner.

I found that *C. alexandra*, like most insects, has a high intrinsic (or inherent) rate of increase [r_m] and thus is capable of reaching large population numbers in a few generations. However, despite the vast potential for egg production revealed under laboratory conditions or by dissection of gravid females, in nature *C. alexandra* is vulnerable to numerous factors which act independently of its population numbers to keep the adult population density relatively low. This is demonstrated by the fact that survivorship to the adult stage is very low (mean survivorship = 1.2%, SD = 1.14; 1975-1979). The proportion of individuals which survive to adult eclosion is relatively constant, thus the larger the number of eggs laid, the larger the resulting number of adults. Key factor analysis of the data has revealed that factors resulting in reduced natality appear to be the most important in determining population trends. Natality is defined as a measure of the ability of the adult females to yield their potential of fertilized eggs (maximum potential natality is calculated by multiplying sex ratio x number of adults x maximum egg production, Fig. 1). For this pop-

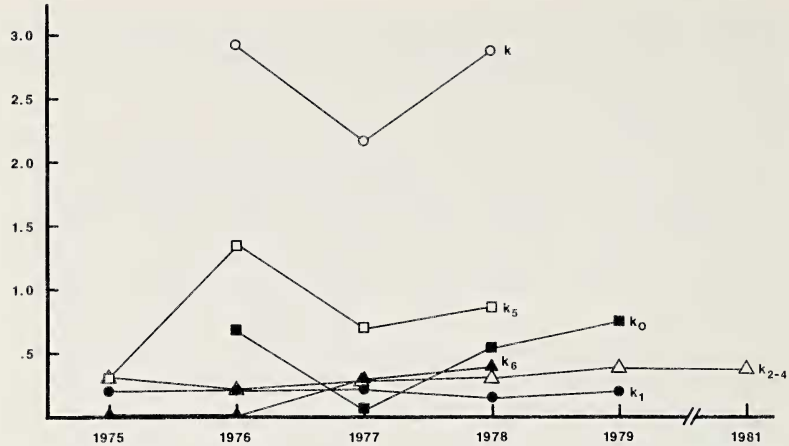

Fig. 1. Graphic presentation of k-factor analysis of life tables for *C. alexandra* 1975-1979, 1981. (k_0 = reduced natality, k_1 = egg mortality, k_{2-4} = pre-diapause larval mortality, k_5 = diapause mortality, k_6 = post-diapause mortality, K = total generation mortality.)

ulation of *C. alexandra* mortality during diapause (dormancy) may also be important, but egg mortality, pre-diapause larval mortality and post-diapause mortality contribute little to the total brood mortality. (In fact, pre-diapause larval mortality is highly negatively correlated to the population trend—a puzzling result which will hopefully be better understood through comparative studies of natural and artificial populations).

Among the factors which result in reduced natality and subsequent population depression are adult removal (e.g. through predation, over-collection, incidental loss to grazers), oviposition interference (e.g. poor weather conditions, interference by courting males) or reduced residence time (e.g. due to loss of nectar sources). The proportion of survivorship may be altered by unusual conditions (e.g. weather extremes, increase or decrease in predation or parasitism) between oviposition periods. These same trends (i.e. reduction of natality with corresponding overall reduction of population size) were found in a similar study of the pierid butterfly *Anthocharis cardamines* (Courtney and Duggan, 1983). A native of the British Isles and continental Europe, *A. cardamines* is a univoltine crucifer-feeding butterfly. Although based on fewer total observations (3 years), the type of data collected and method of analysis were nearly identical to mine. The fact that these techniques yielded similar results when independently applied to the study of a British species verifies the potential for a broader application of both the techniques and conclusions of this study to other species (e.g. Dempster, 1983).

The importance of natality in the study population of *C. alexandra* was

emphasized by incidental experimental manipulation when in 1979 about 30% of the young females in the population were removed (see Graham et al., 1980). As a result, in 1979 egg density in the study area was the lowest observed in the five year period (0.785 eggs/m^2, Fig. 2). The dramatic decrease in population density continued through the next two years. Climatic conditions alone during the two intervening seasons were probably sufficient to account for the further depression of population numbers observed; the number of eggs per unit area fell to 0.36 in 1981 (Fig. 2).

Concurrent with low *C. alexandra* densities during the 1981 season was the nearly explosive increase in numbers of the predaceous mite *Balaustium* sp. This free-living mite had only been previously observed in low numbers in the study area (e.g. Fig. 2; and Ae, 1958). Nymphs of *Balaustium* discover *C. alexandra* eggs, along with other relatively immobile prey items, during an apparently random or patternless search of vegetation surfaces. In 1981, a nearly two-fold increase in egg mortality was observed compared to other years and 65% of all pre-diapause mortality was attributable to this single factor. Year to year fluctuations in stage-specific mortalities of *C. alexandra* had been observed previously, but showed little effect on the overall population trends. However, it seems

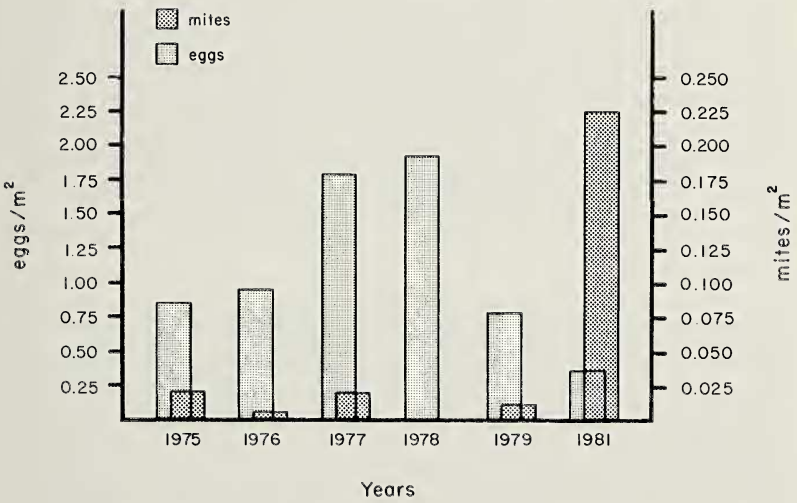

Fig. 2. Histograms for 1975-1979 and 1981 showing both the density of *C. alexandra* as measured by eggs found on the larval food plant *Lathyrus leucanthus* in a 200 m^2 study plot (indicated on the left axis) and the corresponding density of *Balaustrium* as measured by maximum number of mites observed within the study plot during any census period over the season (indicated on the right axis).

likely that excessive egg loss under low density conditions may have a more drastic effect on subsequent population numbers.

The latter prediction is consistent with density dependent population regulation theory (e.g. May et al., 1974; Hassell, 1978). In this traditional view the most significant determinants of population size are factors whose influence varies with population density (e.g. predation). The theory predicts that a lower limit (or threshold number) exists, below which the impact of factors typically considered responsible for year to year population trends will not be important. Since the factors determining the abundance of the *C. alexandra* population are principally density independent (Hayes, 1981b), the findings of this study have important implications for the interpretation of population responses and extrapolation from these events to evaluate whether population regulation is density dependent or independent, or perhaps a combination (see reviews by Dempster, 1983; Strong, 1984).

Survivorship to the diapause stage in 1981 does not suggest any deviation from the typical proportional survivorship schedule of previous years (Fig. 2). A corresponding increase in adult numbers was observed in the field from 1981 to 1982 (W. B. Watt, pers. comm.) and 1983 (pers. obs.). In 1983, a mid-season survey of the population showed an increase in egg number ($> .48/m^2$ compared to the 1981 total of $.36/m^2$), despite the still relatively high mite numbers ($.2/m^2$), which had already caused at least 30% mortality (Hayes, 1984). These results thus fail to verify predictions of population regulation stemming from density dependent theory, but are consistent with my analysis of the 1975-1979 life table data in which variation in natality was identified as the key factor in determining the numbers of this butterfly population (Hayes, 1981b). The interactions of factors which contribute to reduced natality may be more complex than can be accounted for by our current simplistic density-dependent or -independent models of population regulation (e.g. Dempster, 1983; Strong, 1984).

It is very likely that an entirely different picture would have emerged from an examination of predator-prey interaction in 1981 alone, thus underscoring the necessity of long-term studies for the analysis of population dynamics. Despite the extreme effect of the mites on the egg number of *C. alexandra* in the field in 1981, their overall impact on the butterfly population is not significant. The occurrence of epidemic numbers of *Balaustium* was clearly independent of the depressed population number of *C. alexandra*. The opportunistic nature of this predator-prey interaction is evident in the effectively restricted predation by *Balaustium* of only the most immature eggs of *C. alexandra* in addition to the use of a diversity of resources such as pollen (Hayes, 1984).

The butterfly collector or researcher represents a relatively new type of predator to be considered. The analysis presented here suggests that the

extra removal of adults (particularly females) in some years can be devastating, even when population numbers appear to be high (e.g. Watt et al., 1979; also see Ehrlich et al., 1972). Another source of human disturbance is open cattle grazing, which is common throughout most of this region, although the specific effects of such practice on invertebrate populations are not well known. Certainly, the difference in vegetation itself between areas protected from grazing within my study enclosure and outside are quite striking. It may be that cattle have merely replaced the native ungulate herds which were once abundant in the area.

High mortality during egg and larval stages is typical for organisms collectively and simplistically referred to as "r selected" species, a term applied to those organisms which can be characterized by a suite of traits which are associated with high intrinsic rate of growth (reviewed by Stearns, 1976). Pre-adult losses may be as high as 99% of the total number of individuals entering the population (e.g. Dempster, 1973; Williams, 1975). The persistence of "r selected" populations is generally attributed to an environmental uncertainty which is faced by such populations and from which few individuals escape. The overall densities of "r selected" populations are well below the carrying capacity of their current environment and not determined by competition. Mortality due to environmental uncertainty operates in a density-independent fashion so that when any of the sources of mortality relax during the developmental stages, epidemic numbers may be reached in subsequent generations. On the other hand, if adult numbers are reduced (due to reduced natality in the case of *C. alexandra*) resulting in a smaller initial cohort, increased mortality during any developmental stage only contributes to depressing the population further. Populations limited by density-independent factors will therefore only recover slowly from sporadic changes in the mortality schedule.

Conclusion

The above study of *C. alexandra* provides insight into population level interactions (biotic and abiotic) of this species and can serve as a model for others. It is clear that we are only beginning to get a handle on the dynamics of the study population. If we are to achieve a clear perspective of the kinds of factors determining population numbers, populations must be followed for extended periods of time, not simply a few generations. All stages of the life cycle must be considered despite the prominance of a single stage, such as the adult butterfly, or the preeminance of a single mortality factor, such as the stage specific impact of the predacious mite feeding on the eggs of *C. alexandra*. Although five years of data are in many ways just sufficient to begin to draw meaningful conclusions, there are a few studies of such duration. The rapid decline of natural habitat, due to industrialization, urbanization and agricultural

practices, and subsequent loss of natural populations makes our task more urgent. It is only through the continued surveillance of such populations as the above that we can begin to interpret the impact of unpredictable perturbations, such as drought or fire, and the effect of the more predictable and manageable disturbances, such as collecting and grazing.

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